

# Resistance to *Aphis glycines* (Hemiptera: Aphididae) in Various Soybean Lines Under Controlled Laboratory Conditions

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**ABSTRACT** The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), a pest of soybean, *Glycine max* (L.) Merr., native to Asia, has recently become a principal pest of this crop in many areas of North America. Insecticides are currently used to manage *A. glycines*, but host plant resistance is a potential alternative management tool. Tests were conducted to determine resistance to *A. glycines* among soybean lines. ‘Cobb,’ ‘Tie-feng 8,’ and ‘Jackson’ were resistant to population growth of *A. glycines* compared with ‘Cook’ and ‘91B91,’ a susceptible control. Antibiosis was evident in Cobb, Jackson, and Tie-feng 8 from lowered survival of first generation *A. glycines*, and in Cobb, Jackson, Tie-feng 8, and ‘Braxton’ from diminished reproduction by first generation aphids. Antixenosis was apparent in Cobb and Jackson during initial infestation of aphid population growth tests, because *A. glycines* were unsettled and dispersed readily from placement points on unifoliolate leaves. Decreased nymph position by *A. glycines* occurred on Cobb and Jackson, and it may have been caused by antibiotic chemicals in these lines, failure of aphids to settle, or both. Differences in distribution of *A. glycines* between unifoliolate leaves and other shoot structures suggest that unifoliolate leaves were acceptable feeding sites on 91B91 and Cook, whereas unifoliolate leaves and other shoot structures were roughly equally acceptable feeding sites on Braxton, Tie-feng 8, Jackson, and Cobb. However, Jackson and Cobb had relatively low counts of *A. glycines* on shoots that may have been due to abandonment of plants by aphids, decreased aphid survival, or both. Results confirm earlier findings that Jackson is a strong source of resistance to *A. glycines*, and they suggest that Tie-feng 8, Braxton, and especially Cobb are potentially useful sources of resistance.

**KEY WORDS** host plant resistance, PI 436684, PI 548664, antibiosis, antixenosis

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is native to eastern Asia where it is a perennial pest of soybean, *Glycine max* (L.) Merr. (Wang et al. 1996). It was discovered infesting U.S. soybean fields in summer 2000, and it has since spread over the northern soybean-producing region of North America (Venette and Ragsdale 2004). In many areas, large populations of *A. glycines* develop on soybean plants, and they cause yield loss (Myers et al. 2005). *A. glycines* is a vector of several persistently and nonpersistently transmitted viruses of soybean (Clark and Perry 2002, Burrows et al. 2005, Wang et al. 2006), and some of these viruses may cause further yield loss. The impact of *A. glycines* has challenged pest management practitioners to devise environmentally responsible means of protecting soybeans (Rutledge et al. 2004). Currently, insecticides are the recommended means to control *A. glycines* until other management approaches, such as host

plant resistance, are evaluated and developed (Rutledge et al. 2004).

Plant resistance is often the hub of an integrated pest management (IPM) program for insects (Panda and Khush 1995, Wiseman 1999). Limiting infestations of *A. glycines* is a key to preventing yield loss in soybean, and host plant resistance is an effective, economical and environmentally sound strategy to limit insect infestations (Panda and Khush 1995). The three basic modalities of host plant resistance are antixenosis, antibiosis, and tolerance (Painter 1951, Kogan and Ortman 1978, Smith 2005). Antixenosis and antibiosis are measured in terms of aphid responses to host plants, whereas tolerance is measured as differential responses among host plants to specific levels of aphid infestation. Antixenosis deters or reduces colonization by insects, whereas antibiosis causes adverse effects on insect life history. Tolerance is the ability of a plant to grow and reproduce despite supporting an infestation that would limit growth and reproduction of a susceptible host.

Many arthropods, such as aphids, whiteflies, and mites, initially invade crops in low numbers, with populations increasing over several generations before

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Table 1. Soybean lines used in host-plant-resistance experiments with *A. glycines*

Line	Plant introduction no.	Pedigree and comments
Jackson	PI 548657	Volstate(2) × Palmetto (NGRP 2006a); resistant to <i>A. glycines</i> (Hill et al. 2004)
Braxton	PI 533045	F59-1505 × (Bragg(3) × D60-7965) (NGRP 2006a); susceptible to whiteflies (Lambert et al. 1995, 1997)
Cobb	PI 548664	F <sub>5</sub> selection from Braxton × Young (NGRP 2006a); susceptible to whiteflies (Lambert et al. 1995, 1997)
Cook	PI 553045	F57-735 × D58-3358 (NGRP 2006a); resistant to whiteflies (Lambert et al. 1995, 1997)
Tie-feng 8	PI 436684	Tong Zhou Xiao Huang Dou × Jing Shan Pu (Cui et al. 1999); relatively low “grade of resistance” to <i>A. glycines</i> (Fan 1988); susceptible to <i>A. glycines</i> (NGRP 2006b, 2006c)
91B91	None	Pedigree not published; Pioneer Hi-Bred International, Inc. (Johnston, IA); susceptible to <i>A. glycines</i> (Hesler et al. 2007)

reaching damaging levels. For these arthropods, antixenosis and antibiosis can be effective in preventing their populations from reaching economic damage levels (Dreyer and Campbell 1987, Kennedy et al. 1987).

Plant resistance to various insect pests has been identified in many soybean lines (Wiseman 1998, Lambert and Tyler 1999). The screening and identification of sources resistant to *A. glycines* have intensified after the aphid's recent establishment and its economic impact in North American soybean fields, with several lines identified as resistant (Hill et al. 2004, Li et al. 2004, Mensah et al. 2005, Hesler et al. 2007, Diaz-Montano et al. 2006). To date, however, resistance to *A. glycines* is known only for a single dominant gene, *Rag1*, in soybeans ‘Jackson’ and ‘Dowling’ (Hill et al. 2006a, 2006b). Other sources of resistance to *A. glycines* may be needed because crop resistance to aphids from single genes has often been overcome by virulent biotypes within only a few years (Panda and Khush, 1995; Smith, 2005). In this article, we report on identification and characterization of resistance to *A. glycines* in additional soybean lines.

## Materials and Methods

**Overview of Experiments.** We performed four types of growth chamber experiments to compare the responses of *A. glycines* among six soybean lines (Table 1). The four experiments consisted of a screening test and three follow-up experiments to characterize the resistance to *A. glycines* among lines. The variety ‘91B91’ (Pioneer Hi-Bred International, Inc., Johnston, IA) was used as a susceptible control (Hesler et al. 2007), and ‘Jackson’ was used as an *A. glycines*-resistant control (Hill et al. 2004). All experiments were conducted at the North Central Agricultural Research Laboratory, Brookings, SD, in late 2005 and in 2006.

**Plants.** Experimental plants were prepared by placing two seeds of a line into an 8.5-cm square plastic pot filled with a 2:1:1 mixture of soil (fine-loamy, mixed Calcic Hapludolls), perlite, and coarsely ground coconut shells (Coir, J. R. Johnson Supply Inc., Roseville, MN). One week after planting, pots were thinned to one seedling each based on uniform seedling growth. One plant of each line was placed into a 26.5- by 51-cm plastic flat for a total of six line plants per flat. Each flat was used as an experimental block, with experiments set up in a randomized complete block design with

eight or more replications. Experiments commenced by placing large apterous *A. glycines* onto the abaxial surface of expanding unifoliolate leaves of 13- or 14-d-old plants (intermediate VC stage; Pedersen 2004). Experiments were conducted under a photoperiod of 16:8 (L:D) h and 22°C:18°C (L:D) temperature range.

**Aphids.** All *A. glycines* used in the experiments were obtained from a virus-free, multiclonal stock colony maintained on soybean variety ‘Asgrow 0801’ (Monsanto Corp., St. Louis, MO) plants in growth chambers (photoperiod of 16:8 [L:D] h with 22°C:18°C [L:D] temperature range) at our laboratory. The aphid colony was established by collecting aphids from a soybean field in Brookings Co., SD, in summer 2002 and restocked with aphids in summer 2005. Caged aphids were checked every few hours and neonate offspring deposited within the first 30 h were transferred to noninfested plants to ensure that colony plants were free of aphid-transmitted plant virus. Colony plants were maintained 3–4 wk, and then they were infested shoots were clipped and transferred to noninfested, 2-wk-old soybean plants to perpetuate the colony.

**Population Growth Screening Trials.** Lines were screened for resistance in an experiment that rated population growth of *A. glycines* over a 2-wk period by using methods in Hesler et al. (2007). The current experiment commenced by placing five apterous *A. glycines* on the underside of each unifoliolate leaf (10 aphids per individual test plant). Aphids used in the experiment were selected arbitrarily from colony plants, and they were not necessarily uniform in age. After 14 d when plants were in the early V2 stage, they were rated as susceptible to *A. glycines* (>150 aphids per plant) or resistant (<150 aphids per plant) (Hesler et al. 2007). The experiment was repeated, and population ratings for each test were analyzed separately for differences among lines using a two-tailed Fisher exact test (Zar 1998; PROC FREQ, SAS Institute 2002). The proportion of resistant plants per line was compared for each test by using a Tukey-type mean separation for proportions (Zar 1998).

**Distribution of Aphids on and among Plants.** Based on observations of the distribution of *A. glycines* among test lines in the population growth tests, we hypothesized that aphids initially placed on unifoliolate leaves would distribute themselves differentially among lines over time. To test this, we placed five, large apterous *A. glycines* per unifoliolate leaf (10 per plant) without caging. At 24 and 48 h after infesting,

plants were in the late VC stage, and at that time we counted the number of adult aphids on the unifoliolate leaves and elsewhere on the shoots of each plant. Lines were randomized and occurred once within each of 10 replicate blocks. A categorical linear model (Agresti 1990; PROC CATMOD, SAS Institute 2002) was used to test the effect of line, shoot structure (unifoliolate leaves versus other parts of the shoot), and time on the distribution of *A. glycines*.

**No-Choice Nymphiposition Tests.** We hypothesized that differences in the population growth of *A. glycines* among lines stemmed, at least in part, from differential nymphiposition. To test this, we performed two, no-choice nymphiposition tests in which *A. glycines* were confined by clip cage (Hesler et al. 2007) for 24 h (three adults) or 48 h (five adults) per plant. Aphids used in the tests were selected arbitrarily from colony plants and not necessarily uniform in age. They were transferred by small brush from colony plants to test plants. At the end of each test period, the number of nymphs per plant was counted and subjected to analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002).

**Survival, Time to Reproduction, and Number of Progeny.** This experiment was a cohort test (Harris 1980) to determine whether lines affected 1) the survival of *A. glycines* to reproductive maturity, 2) the number of days from birth to onset of reproduction, and 3) the number of nymphs produced by individual *A. glycines* in the first 7 d of adulthood. The experiment was a continuation of the 24-h, no-choice nymphiposition test, and concluded as plants were in the late V1 to early V2 stages. After the number of nymphs per leaf was tallied for the initial 24-h nymphiposition period, aphids were thinned to one neonate per plant and recaged on a unifoliolate leaf. Beginning 5 d later, plants were checked daily for survival and reproductive maturity of the remaining caged aphid. The proportion of aphids that reached reproductive maturity was compared among lines using a Tukey-type multiple comparison test for proportions ( $\alpha = 0.05$ , Zar 1998). The number of days to reproduction was recorded for each aphid, and second generation neonates were counted and removed each day over a 7-d period. The number of days to reproductive maturity was not necessarily normally distributed; therefore, contingency table analysis (chi-square test, PROC FREQ, SAS Institute 2002) was used to test the effect of line on the mean time to reproductive maturity. ANOVA (PROC GLM) was used to test the effect of line on the number of nymphs deposited over 7 d, and treatment means were separated by using Tukey's honest significant difference ( $\alpha = 0.05$ ; Zar 1998).

Results

**Population Growth Screening Tests.** During infestation of test plants, we noticed that aphids on Jackson, 'Cobb,' 'Braxton' and 'Tie-feng 8' dispersed within the initial few minutes from their point of placement on a unifoliolate leaf (e.g., from near mid-vein to leaf edge). In contrast, aphids on 91B91 and 'Cook' gen-

Table 2. Population growth of *A. glycines* among various soybean lines

Line	% plants with >150 <i>A. glycines</i>	
	Test 1	Test 2
91B91	100.0a	87.5a
Cook	100.0a	87.5a
Braxton	37.5ab	62.5a
Cobb	0.0b	0.0b
Tie-feng 8	0.0b	0.0b
Jackson	0.0b	0.0b

Within each column, different letters indicate proportions that differ significantly ( $P < 0.05$ ; Tukey-type multiple comparison test for proportions).

erally remained at the point of placement on a leaf. After 2 wk, differences in population levels of *A. glycines* among lines were generally stark, and ratings of *A. glycines*-population growth differed among lines in each screening test of this experiment (Fisher Exact Test,  $P < 0.0001$ ). In each test, lines 91B91 and Cook had a higher percentage of plants with >150 *A. glycines* than Cobb, Tie-feng 8 and Jackson (Table 2). Braxton had an intermediate percentage of plants with >150 *A. glycines* that did not differ from that of the other lines. Aphids on 91B91 and Cook typically built large populations on unifoliolate leaves, on trifoliolate leaves, and the stem of the first internode, whereas aphids on Cobb, Jackson and Tie-feng 8 were found in relatively low numbers on these structures. Aphids were not distributed consistently among the shoot structures of Braxton test plants.

**Distribution within and among Plants.** The numbers of *A. glycines* on soybean plants differed by line, shoot structure, and the line  $\times$  shoot structure interaction (Table 3). Three groups of lines were evident based on the counts of *A. glycines* and their distribution between unifoliolate leaves and other shoot structures (Fig. 1). Lines 91B91 and Cook had relatively high counts of *A. glycines* distributed mostly on unifoliolate leaves. Braxton and Tie-feng 8 also had relatively high counts of aphids, but aphids were distributed roughly evenly between unifoliolate leaves and other shoot structures. Finally, Jackson and Cobb had relatively low counts of aphids that were distributed

Table 3. Sources of variation in the distribution of *A. glycines* per plant

Source	df	$\chi^2$	P
Line	5	31.86	<0.0001
Shoot structure <sup>a</sup>	1	9.68	0.0019
Time <sup>b</sup>	1	3.48	0.0621
Line $\times$ shoot structure	5	49.95	<0.0001
Line $\times$ time	5	8.64	0.1243
Shoot structure $\times$ time	1	2.97	0.0846
Three-way interaction	5	3.61	0.6075

Results from analysis by categorical log linear model (Agresti 1990; PROC CATMOD, SAS Institute 2002).

<sup>a</sup> Unifoliolate leaves vs stem and trifoliolate leaf.

<sup>b</sup> Twenty-four hours and 48 h after infestation with 10 *A. glycines* per unifoliolate leaves.

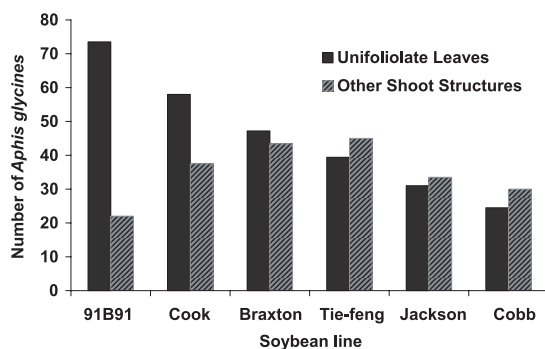


Fig. 1. Number of *A. glycines* on unifoliolate leaves versus other shoot structures among 10 plants each of various soybean lines. Bars represent the mean number of aphids counted at 24 and 48 h after initial infestation with 10 apterous *A. glycines* per plant. Total numbers for each pair of bars per line may not equal 100 aphids due to abandonment of plants by *A. glycines*.

roughly evenly between unifoliolate leaves and other shoot structures.

**No-Choice Nymphiposition Tests.** The number of nymphs deposited by *A. glycines* differed among lines (Table 4) in both the 24-h ( $F = 3.42$ ;  $df = 5, 45$ ;  $P = 0.0106$ ) and 48-h tests ( $F = 4.46$ ;  $df = 5, 45$ ;  $P = 0.0019$ ). In the 24-h test, *A. glycines* deposited fewer nymphs on lines Jackson and Cobb than on 91B91; the number of nymphs on Cook, Tie-feng 8 and Braxton did not differ among these lines or from that on other lines. In the 48-h test, *A. glycines* deposited fewer nymphs on lines Cobb and Jackson than on 91B91 and Cook; the number of nymphs on Tie-feng 8 and Braxton did not differ from each other or from that on other lines.

**Survival, Time to Reproduction, and Number of Progeny.** The proportion of *A. glycines* that reached reproductive maturity varied among lines ( $P < 0.0001$ ; Fisher exact test), with lower proportions of *A. glycines* surviving to reproduce on Jackson (33%), Cobb (42%), and Tie-feng 8 (58%) than on Braxton (83%), 91B91 (100%), and Cook (100%). Lines did not differ in the number of days for *A. glycines* to reach reproductive maturity (mean  $\pm$  SE =  $7.8 \pm 0.2$  d;  $\chi^2 = 6.0$ ,  $df = 6$ ,  $P = 0.30$ ). The number of progeny produced by *A. glycines* differed among lines ( $F = 9.72$ ;  $df = 5, 51$ ;  $P < 0.0001$ ), with fewer progeny on lines Braxton,

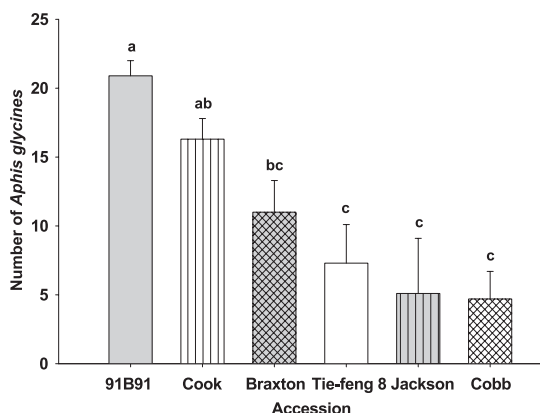


Fig. 2. Comparison of the mean number of progeny produced by apterous *A. glycines* among various soybean lines over the first 7 d of reproduction. Bars with different letters indicate means that differ significantly ( $P < 0.05$ ; Tukey's HSD).

Tie-feng 8, Jackson, and Cobb than on 91B91, and fewer progeny on Tie-feng 8, Jackson, and Cobb than on Cook (Fig. 2).

## Discussion

Our results demonstrated resistance to population growth of *A. glycines* on soybean lines Cobb, Tie-feng 8, and Jackson. Antibiosis and antixenosis are two modalities of resistance that may be responsible for reduced populations of aphids on host plants (Panda and Khush 1995, Smith 2005). Antibiosis was evident in Cobb, Jackson, and Tie-feng 8 from lowered survival of first generation *A. glycines* on these lines, and in Cobb, Jackson, and Tie-feng 8 from diminished reproduction by first generation aphids. Braxton showed nonsignificant reductions in population growth of *A. glycines* in the screening tests, but it still decreased reproduction in first-generation aphids compared with 91B91. Antixenosis was apparent in Cobb and Jackson during initial infestation of aphid population growth tests, because *A. glycines* were unsettled and usually readily dispersed from placement points on unifoliolate leaves of these two lines. Li et al. (2004) also showed decreased survival and reduced fecundity of *A. glycines* on Jackson, and they found that *A. glycines* departed from leaves of Jackson 8–24 h after being placed on them.

Often, however, the expressions of antibiosis and antixenosis overlap, and it may be difficult for experiments to distinguish these two categories of resistance (Panda and Khush 1995, Smith 2005). This was the case in two experiments in our study. For example, the decreased nymphiposition by *A. glycines* on Cobb and Jackson may have been caused by antibiotic chemical(s) in these lines, failure of aphids to settle (antixenosis), or both mechanisms. We observed some dead aphids in clip cages mainly on lines Cobb and Jackson, but it was not clear whether mortality

Table 4. Number of nymphs deposited by five apterous *A. glycines* per plant caged on various soybean lines in two separate tests

Line	Mean $\pm$ SE	
	24-h test	48-h test
91B91	7.0 $\pm$ 1.5a	10.9 $\pm$ 1.1a
Cook	5.2 $\pm$ 0.9ab	11.5 $\pm$ 1.5a
Braxton	5.3 $\pm$ 0.7ab	8.4 $\pm$ 1.2ab
Tie-feng 8	3.9 $\pm$ 0.7ab	9.8 $\pm$ 1.2ab
Cobb	3.3 $\pm$ 0.8b	6.8 $\pm$ 0.8b
Jackson	2.8 $\pm$ 0.5b	6.1 $\pm$ 0.6b

Within each column, different letters indicate means that differ significantly ( $P < 0.05$ ; Tukey's HSD).



was due to toxicity from antibiotic chemicals, dehydration/starvation resulting from antixenosis, or both.

Differences in the distribution of *A. glycines* between unifoliolate leaves and other shoot structures suggest that unifoliolate leaves were acceptable, and perhaps preferred, feeding sites on young plants of 91B91 and Cook, whereas unifoliolate leaves and other shoot structures were roughly equally acceptable feeding sites for aphids on Braxton, Tie-feng 8, Jackson, and Cobb. However, Jackson, and Cobb had relatively low counts of *A. glycines* on shoots, and the low counts may have been due to abandonment of plants by aphids (antixenosis), decreased aphid survival (antibiosis), or both.

Cobb, Braxton, and Tie-feng 8 have been included in previous insect resistance studies. Fan (1988) and Mensah et al. (2005) used a rating scale to score Tie-feng 8 plants based on aphid infestation and plant damage under natural and artificial infestations of *A. glycines*, respectively. Fan (1988) found that Tie-feng 8 was relatively resistant to *A. glycines*, but they did not characterize the nature of its resistance. However, Mensah et al. (2005) found that Tie-feng 8 had relatively high damage indices and that it was susceptible to *A. glycines* under field cage and greenhouse conditions (NGRP 2006b, 2006c).

It is unclear why results with Tie-feng 8 in our study and from Fan (1988) contrast with those of Mensah et al. (2005), but differences may have stemmed from variation within Tie-feng 8 germplasm or in the performance among test populations of *A. glycines*. Seed of Tie-feng 8 in our study and that of Mensah et al. (2005) was obtained originally from Liaoning Province, China, via the Soybean Germplasm Collection (U.S. Department of Agriculture, Urbana, IL), and this source lists Tie-feng 8 as a pureline, cultivated material (NGRP 2006a). The relation of this seed to the particular Tie-feng 8 seed used by Fan (1988) is unknown, but Fan was based at a research facility in Liaoning Province. Thus, Tie-feng 8 germplasm may be common among the three studies.

Alternatively, performance of particular test colonies of *A. glycines* with regard to Tie-feng 8 may have differed among the studies. *A. glycines* in Fan (1988) and the *A. glycines* colony that we used did not survive and reproduce well on Tie-feng 8, whereas *A. glycines* readily built large populations in the study by Mensah et al. (2005). The population genetics of *A. glycines* have not been compared between Chinese and North American populations, but this comparison may be warranted to understand differential performance of *A. glycines* on Tie-feng 8 and its implications for managing resistant soybean lines.

Plants in the current study were tested in the early vegetative stages of development. However, some soybean lines with strong resistance to *A. glycines* in early vegetative stages may nevertheless suffer declines in height, dry mass, and yield after long exposure to aphids compared with protected plants (Hill et al. 2004). Mensah et al. (2005) found low correlation between number of *A. glycines* per soybean leaflet 10 d after inoculation and a plant damage index 4 wk after

inoculation. Thus, testing of resistant lines such as Cobb, Tie-feng 8, and Braxton against *A. glycines* is needed to determine whether resistance can preclude declines in plant growth and yield after aphid infestation for extended duration or during later plant growth stages.

Lines Cobb and Braxton were resistant and Cook was susceptible to *A. glycines* in our study, but Lambert et al. (1995, 1997) found that Cook was resistant and Cobb and Braxton were susceptible to whiteflies *Bemisia tabaci* (Gennadius) and *Trialeurodes abutilonea* (Haldeman) (Homoptera: Aleyrodidae). Lambert et al. (1995) determined that whitefly population levels on 14 soybean lines were correlated with erectness of leaf trichomes. Our limited results suggest that whitefly resistance in soybean is inversely related to *A. glycines* resistance, but this generalization is based on only three lines that have been tested against both whiteflies and aphids. Further experiments are needed to test for a relationship between trichome erectness and resistance to *A. glycines*.

There are now several sources of soybean that have been identified with resistance to *A. glycines* (Hill et al. 2004, Li et al. 2004, Mensah et al. 2005, Hesler et al. 2007, Diaz-Montano et al. 2006; this study). Cobb could be readily included in programs to breed soybean with resistance to *A. glycines*. Braxton seems to have some individuals with moderate antibiosis resistance to *A. glycines*, and further selection for resistant lines within Braxton is needed. Tie-feng 8 showed strong antibiosis to *A. glycines* in our tests, but it must be further evaluated for its use in breeding for aphid resistance in light of results by Mensah et al. (2005). The various sources of resistance to *A. glycines* may lead to the eventual deployment of aphid-resistant cultivars. Such a development may greatly lessen the frequency of aphicide application and thereby reduce economic and environmental costs of managing *A. glycines* in soybean production systems.

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### References Cited

- Agresti, A. 1990. Categorical data analysis. Wiley, New York.
- Burrows, M.E.L., C. M. Boorerboom, J. M. Gaska, and C. R. Gau. 2005. The relationship between *Aphis glycines* and *Soybean mosaic virus* incidence in different pest management systems. *Plant Dis.* 89: 926–934.
- Clark, A. J., and K. L. Perry. 2002. Transmissibility of field isolates of soybean viruses by *Aphis glycines*. *Plant Dis.* 86: 1219–1222.
- Cui, Z., T. E. Carter, Jr., J. Gai, J. Qui, and R. L. Nelson. 1999. Origin, description, and pedigree of Chinese soybean cultivars released from 1923 to 1995. Technical Bulletin

- No. 1871. U.S. Department of Agriculture–Agricultural Research Service, Washington, DC.
- Diaz-Montano, J., J. C. Reese, W. T. Schapaugh, and L. R. Campbell. 2006. Characterization of antibiosis and antixenosis to the soybean aphid (Hemiptera: Aphididae) in several soybean genotypes. *J. Econ. Entomol.* 99: 1884–1889.
- Dreyer, D. L., and B. C. Campbell. 1987. Chemical basis of host-plant resistance to aphids. *Plant Cell Environ.* 10: 353–361.
- Fan, Y. 1988. Screening for soybean varieties resistant to soybean aphid. *Soybean Sci.* 7: 167–169.
- Harris, M. K. 1980. Arthropod-plant interactions related to agriculture, emphasizing host plant resistance. In M. K. Harris [ed.], *Biology and breeding for resistance to arthropods and pathogens in agricultural plants*. Texas Agricultural Experiment Station, Texas A&M University, College Station, TX, and Agency for International Development, University of California, Berkeley, CA.
- Hesler, L. S., K. E. Dashiell, and J. G. Lundgren. 2007. Antibiosis and antixenosis to *Aphis glycines* in soybean accessions. *Euphytica* 154: 91–99.
- Hill, C. B., Y. Li, and G. L. Hartman. 2004. Resistance to the soybean aphid in soybean germplasm. *Crop Sci.* 44: 98–106.
- Hill, C. B., Y. Li, and G. L. Hartman. 2006a. A single dominant gene for resistance to the soybean aphid in the soybean cultivar Dowling. *Crop Sci.* 46: 1601–1605.
- Hill, C. B., Y. Li, and G. L. Hartman. 2006b. Soybean aphid resistance in soybean Jackson is controlled by a single dominant gene. *Crop Sci.* 46: 1606–1608.
- Kennedy, G. G., F. Gould, O. M. B. Deponti, and R. E. Stinner. 1987. Ecological, agricultural, genetic, and commercial considerations in the deployment of insect-resistant germplasm. *Environ. Entomol.* 16: 327–338.
- Kogan, M., and E. E. Ortman. 1978. Antixenosis—a new term proposed to replace Painter's 'nonpreference' modality of resistance. *Bull. Entomol. Soc. Am.* 24: 175–176.
- Lambert, A. L., and J. Tyler. 1999. Appraisal of insect-resistant soybeans. In B. R. Wiseman and J. A. Webster [eds.], *Economic, environmental, and social benefits of resistance in field crops*. In Proceedings Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD.
- Lambert, A. L., R. M. McPherson, and K. E. Espelie. 1995. Soybean host plant resistance mechanisms that alter abundance of whiteflies (Homoptera: Aleyrodidae). *Environ. Entomol.* 24: 1381–1386.
- Lambert, A. L., R. M. McPherson, and G. A. Herzog. 1997. Field evaluation of fourteen soybean genotypes for resistance to whitefly (Homoptera: Aleyrodidae) infestations. *J. Econ. Entomol.* 90: 658–662.
- Li, Y., C. B. Hill, and G. L. Hartman. 2004. Effect of three resistant soybean genotypes on the fecundity, mortality, and maturation of soybean aphid (Homoptera: Aphididae). *J. Econ. Entomol.* 97: 1106–1111.
- Mensah, C., C. DiFonzo, R. L. Nelson, and D. Wong. 2005. Resistance to soybean aphid in early maturing soybean germplasm. *Crop Sci.* 45: 2228–2233.
- Myers, S. W., C. Gratton, R. P. Wolkowski, D. B. Hogg, and J. L. Wedberg. 2005. Effect of soil potassium availability on soybean aphid (Hemiptera: Aphididae) population dynamics and soybean yield. *J. Econ. Entomol.* 98: 113–120.
- [NGRP] National Genetic Resources Program. 2006a. U.S. Department of Agriculture, Germplasm Resources Information Network. National Germplasm Resources Laboratory, Beltsville, MD. ([http://www.ars-grin.gov/npgs/acc/acc\\_queries.html](http://www.ars-grin.gov/npgs/acc/acc_queries.html)).
- [NGRP] National Genetic Resources Program. 2006b. U.S. Department of Agriculture, Germplasm Resources Information Network. National Germplasm Resources Laboratory, Beltsville, MD. ([http://www.ars-grin.gov/cgi-bin/npgs/html/dno\\_eval\\_acc.pl?51111+493028+983](http://www.ars-grin.gov/cgi-bin/npgs/html/dno_eval_acc.pl?51111+493028+983)).
- [NGRP] National Genetic Resources Program. 2006c. U.S. Department of Agriculture, Germplasm Resources Information Network. National Germplasm Resources Laboratory, Beltsville, MD. ([http://www.ars-grin.gov/cgi-bin/npgs/html/dno\\_eval\\_acc.pl?51111+493029+873](http://www.ars-grin.gov/cgi-bin/npgs/html/dno_eval_acc.pl?51111+493029+873)).
- Painter, W. H. 1951. *Insect resistance in crop plants*. Macmillan, New York.
- Panda, N., and G. S. Khush. 1995. *Host plant resistance to insects*. CAB International, Oxon, United Kingdom.
- Pedersen, P. 2004. *Soybean growth and development*. Publication PM 1945, University Extension, Iowa State University, Ames, IA.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240–248.
- SAS Institute. 2002. *SAS proprietary software, version 9.1*. SAS Institute, Cary, NC.
- Smith, C. M. 2005. *Plant resistance to arthropods*. Springer, Dordrecht, The Netherlands.
- Venette, R. C., and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? *Ann. Entomol. Soc. Am.* 97: 219–225.
- Wang, S. Y., X. Z. Bao, Y. J. Sun, R. L. Chen, and B. P. Zhai. 1996. Effect of population dynamics of the soybean aphid (*Aphis glycines*) on soybean growth and yield. *Soybean Sci.* 15: 243–247.
- Wang, R. Y., A. Kritzman, D. E. Hershman, S. A. Ghabrial. 2006. *Aphis glycines* as a vector of persistently and non-persistently transmitted viruses and potential risks for soybean and other crops. *Plant Dis.* 90: 920–926.
- Wiseman, B. R. 1998. Assessment of soybean germplasm for multiple insect resistance. In S. L. Clement and S. S. Quisenberry [eds.], *Global plant and genetic resources for insect-resistant crops*. CRC, Boca Raton, FL.
- Wiseman, B. R. 1999. Successes in plant resistance to insects. In B. R. Wiseman and J. A. Webster [eds.], *Economic, environmental, and social benefits of resistance in field crops*. Proceedings Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD.
- Zar, J. H. 1998. *Biostatistical analysis*, 4th ed. Prentice Hall, Upper Saddle River, NJ.

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